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SEASONAL VARIATION OF BLACK PIGMENTATION UNDER THE WINGS IN A TRUE BUG (HEMIPTERA: PENTATOMIDAE): A LABORATORY AND FIELD STUDY[1]

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Abstract.—In adults of the predaceous hemipteran, *Podisus maculiventris* (Pentatomidae), the abdominal terga vary from having no black pigment to being entirely black. Examination of wild *P. maculiventris* adults collected in pheromone-baited traps showed that black pigmentation of the tergum is most extensive in adults collected in fall and spring, and minimal in adults collected in midsummer. Topical treatment of 1-day-old fifth-stage *P. maculiventris* larvae with juvenile hormone inhibited tergal blackening following ecdysis to the adult stage, suggesting that the black pigment is a true melanin. Under laboratory conditions, higher rearing temperatures inhibited melanization but photoperiod had little or no effect on the melanization of *P. maculiventris* adults. At any particular rearing temperature or field-collection date, the terga of females were significantly darker than the terga of males, but the melanization of males varied more than that of females over a range of rearing temperatures or collection dates. Body size was at most only weakly correlated with the degree of melanization in wild and laboratory-reared *P. maculiventris* males and females. The adaptive significance of melanism in *P. maculiventris* is discussed.

Variation in the cuticular melanization of insects is widespread (Kalmus, 1941a). Familiar examples include hyper-melanization of certain moths near smoke-polluted industrial centers (Kettlewell, 1961), geographical variation in the black elytral spots of ladybird beetles (Brakefield, 1984), and annual variability in the black bands of woollybear caterpillars thought by some to predict the severity of the coming winter (Borror et al., 1981). In this paper I will describe the melanism of adult spined soldier bugs, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), and examine possible causes of melanic variation in this true bug.

The most thorough study of color variation in an hemipteran insect was conducted by Knight (1923, 1924) on the twospotted stink bug, *Perillus bioculatus* (F.) (Pentatomidae). In *P. bioculatus* adults black and brown pigments are located in the cuticle and do not appreciably change after the initial hardening of the cuticle. The white, yellow and red colors are located in the epidermis and show through where the cuticle is transparent. The proportion of melanized and trans-

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parent cuticle in *P. bioculatus* adults is regulated by temperature and only slightly affected by humidity; cooler rearing temperatures increase the area of melanized cuticle (Knight, 1924). Similarly, Novak (1955) found that the melanized sternal spots of adult milkweed bugs, *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae), are larger when the bugs are reared at lower temperatures, and that at the same rearing temperature the extent of melanization is greater in females than males. Knight (1923) reported that field collections of *P. bioculatus* corroborated his laboratory findings on the effect of temperature on melanization, and Dupuis (1949) noticed that larvae of several pentatomids are melanic when collected late in the season, but these observations were based upon relatively few field-collected specimens. Couturier (1938) reported that the black pigmentation of laboratory-reared fifth-stage *P. maculiventris* larvae was extremely variable, but he noticed no obvious differences in the pigmentation of adults. The availability of an artificial pheromone for the spined soldier bug (Aldrich et al., 1984) made possible a detailed examination of the seasonal melanic variation of wild *P. maculiventris* males and females. The ability to easily rear large numbers of this insect (Aldrich et al., 1978) enabled me to study the environmental and hormonal causes of *P. maculiventris* melanism in the laboratory.

Methods and Materials

Podisus maculiventris adults were caught in pheromone-baited traps near the Insect Physiology Laboratory, Beltsville Agricultural Research Center, from May, 1982, through April, 1985. Traps were deployed and pheromone prepared as previously described (Aldrich et al., 1984). Captured spined soldier bugs were stored in 70% ethanol or pinned for later scoring of melanization (Fig. 1). In 1982 and 1983, the width of the third abdominal tergite (excluding the connexiva) of melanically scored field-collected *P. maculiventris* adults was measured under a dissecting microscope to 0.1 mm using a mini-scale℠ (BioQuip Products, Santa Monica, CA). In April of 1984 and 1985, the melanically scored field-collected *P. maculiventris* adults were weighed to an accuracy of 0.1 mg. Daily temperature data were obtained from the United States weather station at the research center, approximately 3 kilometers from the study site.

Laboratory investigations were conducted on bugs from a stock colony started with individuals collected at the research center in 1982. The stock colony was maintained on *Tenebrio molitor* L. pupae (Coleoptera: Tenebrionidae) (Rainbow Mealworms, Compton, CA) at 26.7 ± 1.5°C, 65% relative humidity (RH), and a 16:8 h light : dark (L:D) photoperiod. The critical period for commitment to melanization was determined by transferring fourth- and fifth-stage larvae of known age from the stock colony to an unlighted rearing chamber at 15.5°C and correlating adult melanism with the age of the larvae when transferred.

To test the effect of photoperiod on adult melanism, fourth instars were reared to the adult stage at reversed photoperiods but otherwise identical conditions. Two light-proof cabinets (46 × 31 × 107 cm) built one on top of the other inside a walk-in insectary (29.4 ± 2.8°C) were used for this experiment. Each cabinet was equipped with a fluorescent light (Sylvania F14T12-CW; 675 lumens); the top cabinet was cycled at 8:16 h L:D and the bottom cabinet was cycled at 16:8 h L:D. Hygrothermographs (Belfort Instrument Co., Baltimore, MD) were run simultaneously in each cabinet during the experiments.

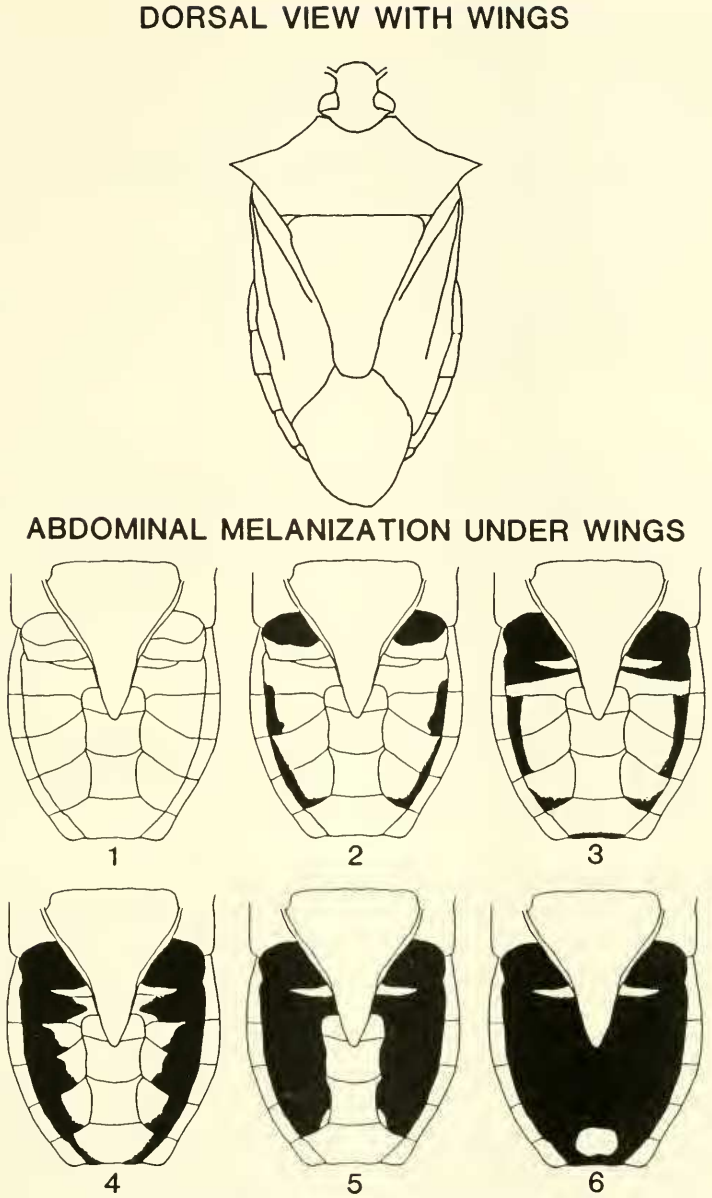

Fig. 1. Dorsal view of adult *Podisus maculiventris* with wings intact (top) and with wings removed (bottom). The abdominal melanization of adults was scored from unmelanized (score = 1) to almost entirely melanized (score = 6).

The effect of temperature on adult melanism was examined by rearing late fourth-stage larvae at 15.5, 21.1, 26.7 or 32.2°C. Larvae reared at 21.1, 26.7 and 32.2°C were housed in insectaries with 16:8 h L:D cycles, 65 ± 5% RH, and temperature fluctuations of ≤1.5°C. Larvae reared at 15.5°C were housed in an unlighted box at ambient RH with temperature fluctuations of ≤2.5°C. One set

of larvae was reared in the unlighted box at 35.8 ± 4.7°C to check for a photoperiodic effect on adult melanism.

Since melanization in some insects is inhibited by juvenile hormone (JH) (e.g. Truman et al., 1973), the effect of JH on the tergal melanization of *P. maculiventris* adults was tested. Female fifth-stage larvae (24 ± 8 h post-ecdysis) were removed from the stock colony, lightly anesthetized with CO_2, and topically treated with 5, 0.5 or 0.05 μg JH-1 (methyl *cis*-10,11-epoxy-7-ethyl-3,11-dimethyl-*trans, trans*-2,6-tridecadienoate; Ayerst Laboratories, Montreal, Canada) in 1 μl of acetone. CO_2-Anesthetized, acetone treated controls were run simultaneously with each set of treatments. Treated and control larvae were reared to the adult stage at 26.7°C, 16:8 h L:D and 65% RH. The area of melanized tergal cuticle of each adult was scored on the scale shown in Figure 1.

Results

Field data.—From May, 1982, through April, 1985, a total of 4800 *P. maculiventris* adults were caught in or near pheromone-baited traps. Spined soldier bugs overwinter as adults and, at our study site, begin emerging in early April (Fig. 2, 1983). *Podisus maculiventris* larvae are occasionally caught in pheromone-baited traps (Aldrich, 1985), and third, fourth and fifth instars have been caught from mid-April to mid-May, demonstrating that overwintered adult females oviposit soon after emergence (Aldrich, unpubl. data). The first new generation of adults (F_1) appears from late May through June, followed by 1 or 2 more overlapping generations (Fig. 2, 1982 and 1983). About 10% of the adult bugs that emerge in the spring contain a larva of the tachinid fly parasitoid, *Hemyda aurata* Robineau-Desvoidy. Another tachinid, *Euclytia flava* (Townsend), parasitizes virtually all *P. maculiventris* adults caught in traps beginning about 2 weeks after the bugs emerge and, in fact, causes the bugs to avoid traps (Aldrich et al., 1984). Thus, the adults captured from late May through June must be predominantly newly ecdysed (F_1) adults because most of the overwintered adults probably do not survive beyond May.

From May, 1982, through April, 1985, a total of 1968 wild spined soldier bug adults were scored for tergal melanism and either measured or weighed. The abdominal terga of these adult spined soldier bugs varied from unmelanized to completely melanized (Fig. 1). Unmelanized tergal cuticle is translucent and appears brownish orange. As is characteristic of alate Hemiptera, the abdominal tergum of a *P. maculiventris* adult is covered by the wings except during flight (Fig. 1, top). There are thus no obvious differences in the coloration of adults having varying tergal melanization; dorsally the adults are dull yellow with small fuscous punctures and ventrally they are pale yellow with small reddish punctures (Blatchley, 1926).

Plotting the abdominal melanization score versus the collection date of male and female *P. maculiventris* adults reveals two important features of the population (Fig. 3). First, for adults collected at the same date, females are on the average more extensively melanized than males. Second, adults collected in the spring are more extensively melanized than those collected in the summer. The decline in tergal melanism with the advancing season, however, is not coincident with the appearance of the F_1 generation of adults. For example, in 1983 the transition in the melanization of field-collected bugs occurred from mid-June to

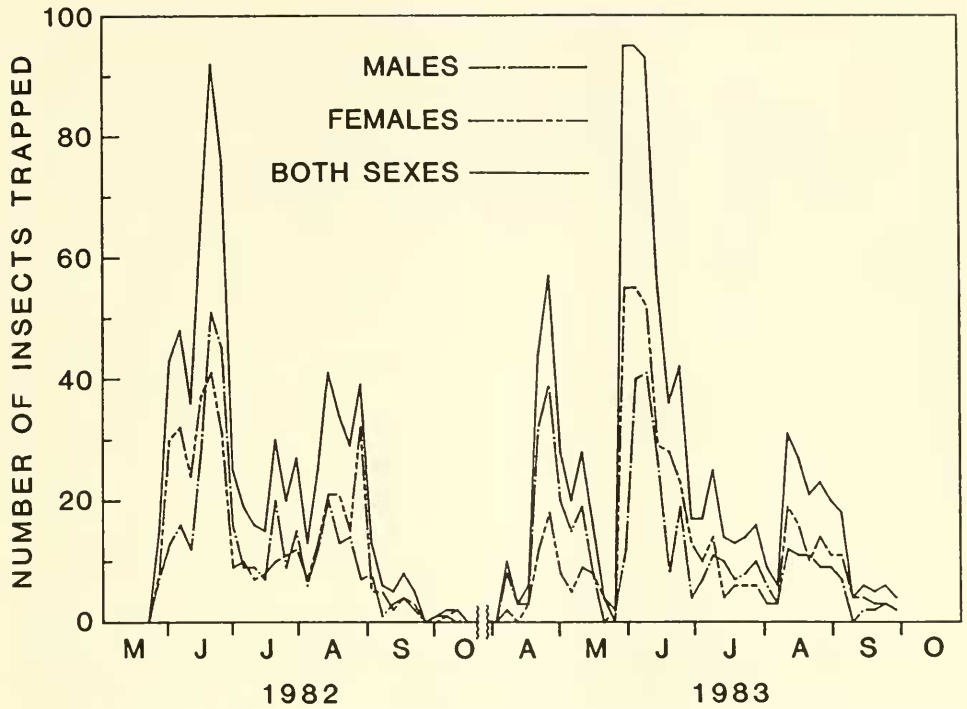

Fig. 2. *Podisus maculiventris* adults caught in or within 1 m of pheromone-baited traps monitored daily at the Agricultural Research Center, Beltsville, Maryland, during 1982 and 1983. Each point is a 5-day summation of the catches from seven sticky-wing traps.

mid-July (Fig. 3), but the peak collection of new adults occurred during late May and early June (Fig. 2). At the end of the trapping season the degree of tergal melanization and the confidence intervals for these points increased, but overwintered males and females were, on the average, more melanized than the adults caught the preceding September and October (Fig. 3).

The reduction in tergal melanism of *P. maculiventris* adults collected in May and June coincides with increasing daily temperatures during this period (Fig. 4). Prior to May 31, 1983, mean daily temperatures seldom exceeded 23.3°C (the transitional melanization temperature calculated from laboratory rearing data), whereas in June, July and August the daily mean temperature usually exceeded 23.3°C (Fig. 4). In September, mean daily temperatures were again below the transitional melanization temperature (Fig. 4), coinciding with the increase in the melanism of adults caught in September, 1983 (Fig. 3). The temperature curves for 1982 and 1984 exhibit patterns similar to that shown in Figure 4 for 1983, however, there were significant differences in the temperature extremes and the precise timing of temperature shifts from year to year. For example, during the period from August 15 through September 30 there were 40, 27 and 36 days when the mean daily temperature was 23.3°C or less in 1982, 1983 and 1984, respectively. Even though data for only 3 years are available, the correlation coefficient between the number of days $\leq$23.3°C from August 15 through September 30 and the melanization score of males collected the following April was significant (r =

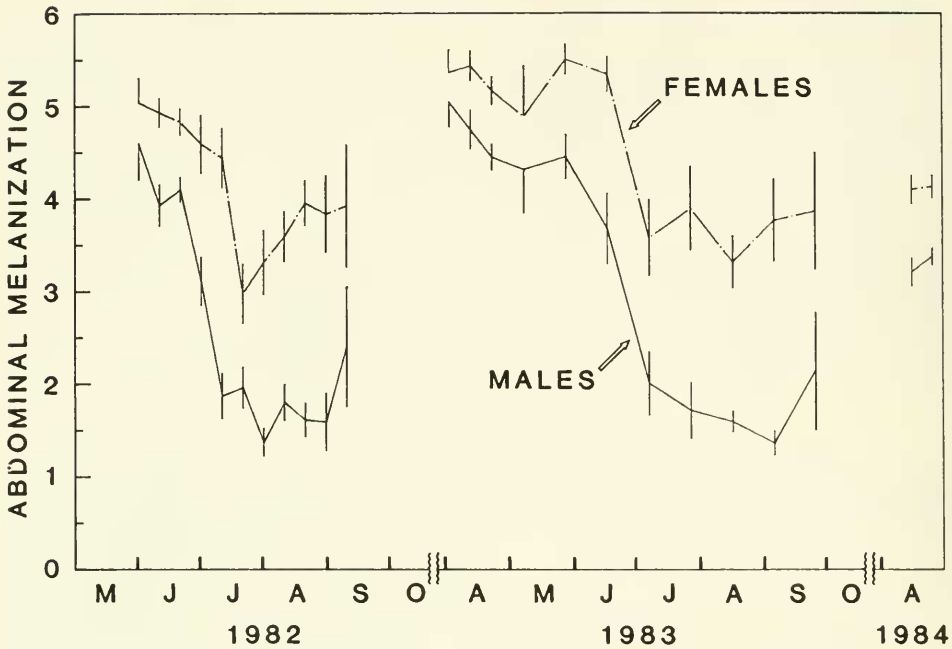

Fig. 3. A plot of melanization score versus collection date for *Podisus maculiventris* adults captured in or near pheromone-baited traps from May 1982 through April 1984.

0.9999, $P < 0.05$; melanization scores = 4.59, 3.32 and 4.18, respectively). For females this correlation was not significant (r = 0.9516; melanization scores = 5.27, 4.11 and 5.28, respectively).

Field-collected *P. maculiventris* females are significantly larger than males. For example, 95 females trapped April 17 through 19, 1984, weighed 47.4 ± 0.8 mg ($\bar{x}$ ± SEM), and 97 males trapped during the same period weighed 36.0 ± 0.6 mg (t = 11.247, $P < 0.001$). Based on the width of the third tergite, females were larger than males and there was a tendency for larger individuals to survive the winter; the width of females collected August 1 through September 24, 1982, was 4.75 ± 0.02 mm ($\bar{x}$ ± SEM, n = 247) versus 4.79 ± 0.02 mm (n = 133) for females collected April 3 through May 14, 1983, and the widths of males collected during the same periods, respectively, were 4.31 ± 0.02 mm (n = 187) and 4.33 ± 0.01 mm (n = 227). However, body size was never significantly correlated with the degree of melanization in field-collected bugs; e.g. r = 0.0420 (n = 149) for females and r = 0.0064 (n = 268) for males collected March 28 through April 21, 1985.

Laboratory data.—Transferring larvae of various ages from warm to cool rearing chambers indicated that the critical period for determination of adult melanism is approximately 24 h after ecdysis from the fourth to the fifth stage. Melanization of the abdominal tergum in *P. maculiventris* adults is first evident about 2 h after ecdysis. By 6 h post-ecdysis the final tergal melanization score can be discerned. After about 12 h, melanization of the tergum appears to be complete and does not visibly change for the rest of the life of the insect.

Rearing *P. maculiventris* larvae under reversed photoperiods had little or no

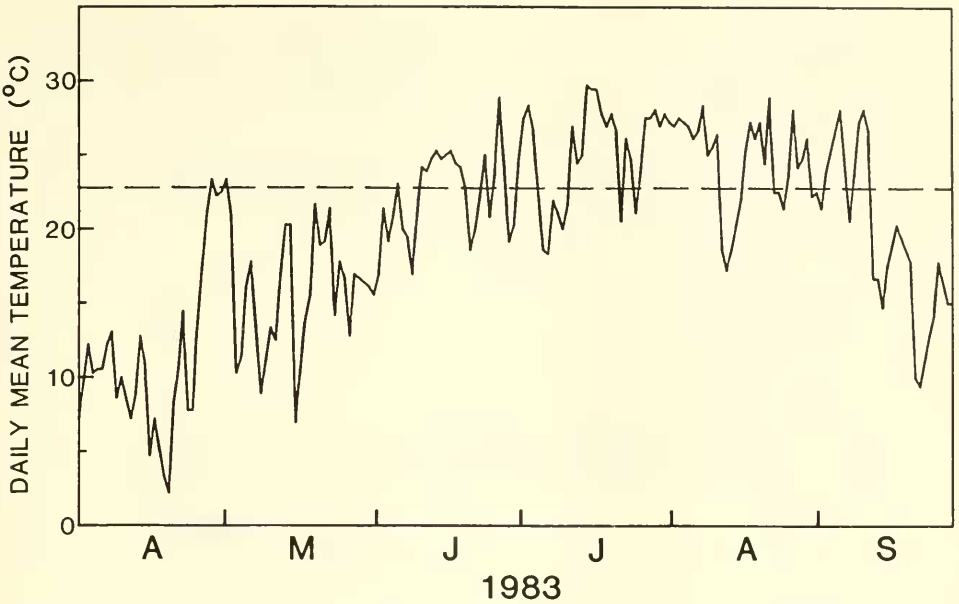

Fig. 4. Daily mean temperatures from April through September, 1983. The broken isothermal line is at 23.3°C, the transitional temperature for melanization in *Podisus maculiventris* adults.

effect on the melanism of adults (Fig. 5). For males reared at 16:8 h L:D (n = 180) there were about 5.5% more unmelanized individuals (score = 1) than for males reared at 8:16 h L:D (n = 156) (Fig. 5A). For females reared at 16:8 h L:D (n = 179) there were about 6.1% more individuals with melanization scores ≤ 3 than for females reared at 8:16 h L:D (n = 172) (Fig. 5B). The small excess of lighter adults under long-day conditions may be entirely due to the slight warming of the rearing cabinet caused by the longer light-on time. This experiment also demonstrated that at the same rearing temperature, in this case 29.4°C, the resulting tergal melanism of adult females ($\bar{x} \pm$ SEM = 3.45 $\pm$ 0.09, n = 351) is greater than that of males (1.18 $\pm$ 0.03, n = 336).

The relationship of body weight to melanism for 576 *P. maculiventris* fourth-stage larvae reared to the adult stage at 26.7°C under long-day conditions is shown in Fig. 6. Over 85% of the males had a melanization score ≤ 3 at this rearing temperature and there is virtually no correlation between body weight and melanism (Fig. 6B). To the contrary, fewer than 8% of the females had a melanization score ≤ 3 and there is a significant positive correlation between body weight and melanism ($P < 0.01$) (Fig. 6A). Regression of body weight on melanism score reveals that body weight accounts for at most 8% ($r^2 = 0.0791$) of the natural melanic variation. As with field-collected bugs, laboratory-reared female bugs are larger than males (77.2 $\pm$ 1.0 mg and 52.9 $\pm$ 0.6 mg, respectively), but these laboratory-reared adults were much larger than overwintered field-collected *P. manculiventris* individuals.

The temperature at which late-stage *P. maculiventris* larvae are reared has a pronounced effect on the tergal melanism expressed in the adult stage (Fig. 7). At a given rearing temperature females are, on the average, more melanized than

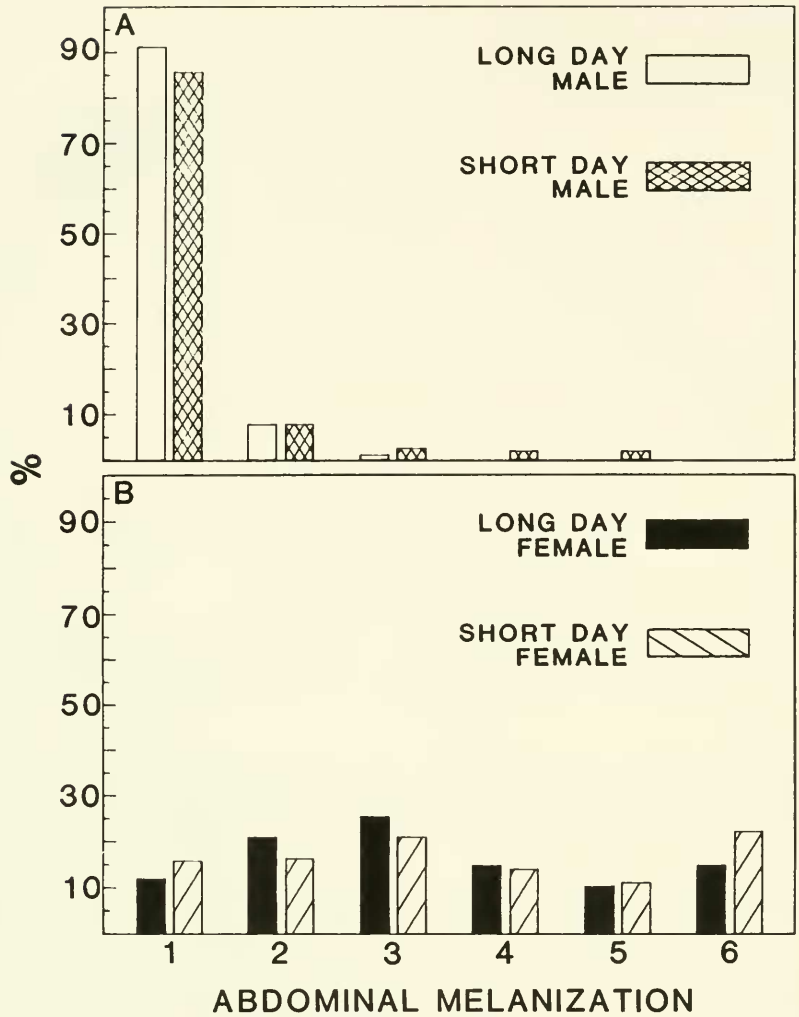

Fig. 5. Histogram of abdominal melanization for *Podisus maculiventris* adults reared at 29.4°C under either a long-day (16:8 h L:D) or a short-day (8:16 h L:D) photoperiod; A, males, B, females.

males. However, at different rearing temperatures the range of female melanization scores was relatively narrow, from 5.69 ± 0.17 at 15.5°C to 3.76 ± 0.15 at 32.2°C. On the other hand, the range of tergal melanism in males was much greater, from 4.82 ± 0.16 at 15.5°C to 1.21 ± 0.07 at 32.2°C. Although males are much more melanically variable than females, the average of the melanism range for each sex as plotted in Fig. 7 (i.e. score = 3 for males; score = 5 for females) falls at almost exactly the same temperature, 23.3°C. Therefore, 23.3°C has been considered the transitional melanization temperature for both sexes of *P. maculiventris* (Fig. 4).

Rearing fourth-stage larvae to the adult stage at 35.8°C in continual darkness produced unmelanized males (1.10 ± 0.08, n = 29) and lightly melanized females (2.17 ± 0.24, n = 24), verifying that temperature and not photoperiod is the primary determinant of adult melanism.

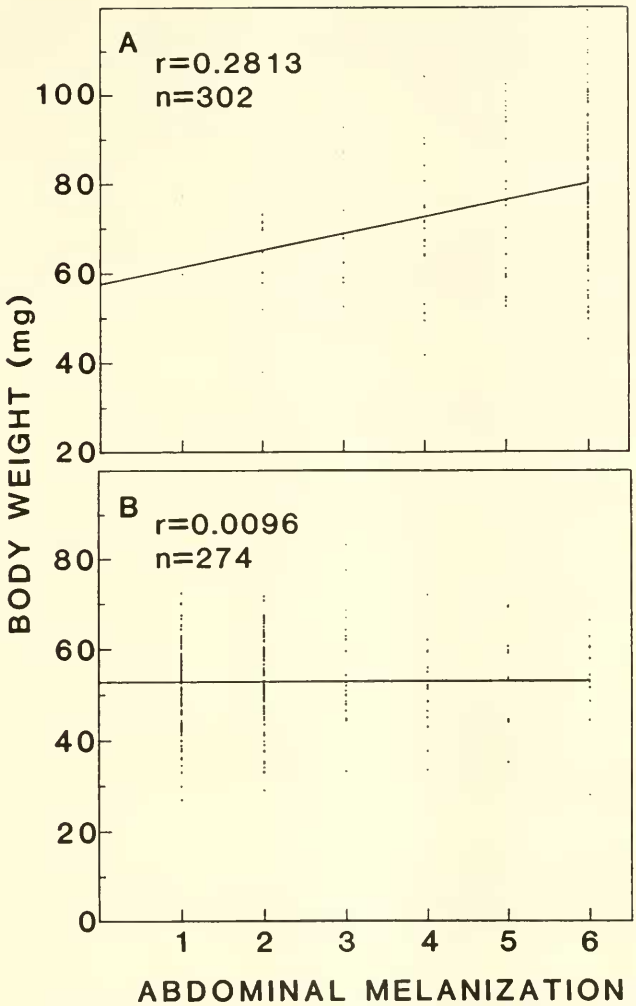

Fig. 6. Scatter plots of body weight versus melanization score for female (A) and male (B) *Podisus maculiventris* adults laboratory reared at 26.7°C and a 16:8 h L:D photoperiod (each point corresponds to one insect). Note the higher weight scale for females than for males.

Topical treatment of 24-h-old female fifth-instar *P. maculiventris* larvae with JH-1 inhibited melanization in the adult stage (Table 1). At a dose of 5 μg JH-1, most larvae failed to successfully molt and some that did exhibited juvenile characters. None of the 6 individuals which succeeded in molting normally after treatment with 5 μg JH-1 had any melanization of the abdominal tergum. At the 0.5-μg dose, adult tergal melanization was inhibited by 37% relative to controls. Furthermore, at this intermediate JH dose most individuals showing some degree of melanization had patches of unmelanized cuticle in otherwise melanized cuticular areas, creating a mottled appearance. Treatment with 0.05 μg JH-1 also significantly inhibited the area of the tergum melanized, but mottling of the melanic areas was infrequent. Although tergal pigmentation was inhibited by JH,

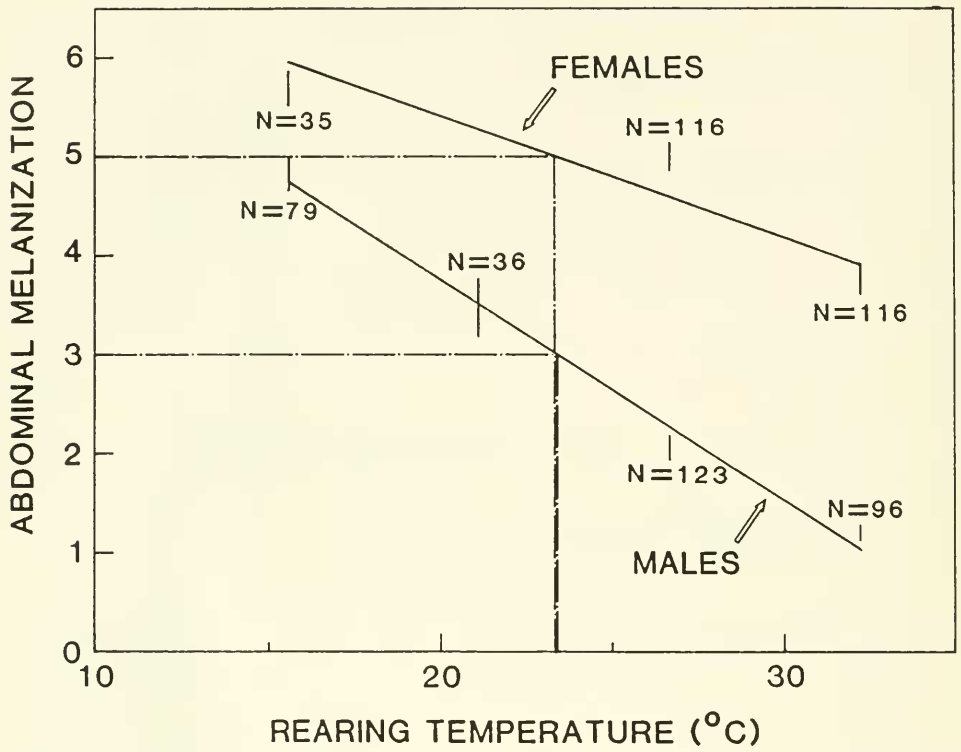

Fig. 7. The effect of rearing temperature on the abdominal melanization of adult male and female *Podisus maculiventris* under long-day conditions. Bars through points are standard errors of the means.

normal sclerotization of the cuticle was apparently unaffected; adults treated as larvae were mobile, fed normally and were long-lived.

Discussion

Not all black pigments in insects are melanins (Kayser, 1985). Sclerotization can produce black cuticles in insects (Andersen, 1985), and melanization and sclerotization of cuticles are two independent processes in insects (Kayser, 1985). Rigorous proof of the existence of true melanins has been provided for only a few species and the black tergal pigment described here in *P. maculiventris* has yet to be chemically characterized. However, the inhibition of tergal pigmentation in adult spined soldier bugs by JH, with a critical period long before the onset of pigmentation, is similar to the pigmentation process in larvae of black mutant *Manduca sexta* (L.) (Lepidoptera: Sphingidae) (Truman et al., 1973), an insect shown to be truly melanic (Hori et al., 1984). The mottled appearance of the tergum in JH-treated *P. maculiventris* adults suggests that the black pigment is formed in discrete granules, another feature of melanization in black mutant *M. sexta* larvae (Curtis et al., 1984) and many truly melanic insects (Kayser, 1985). Furthermore, JH treatment did not inhibit sclerotization in *P. maculiventris* adults. Melanins in insect cuticle have only been found in the exocuticular part that is shed at ecdysis (Kayser, 1985). When adult milkweed bugs were artificially induced to molt by injection of an ecdysteroid, the exuviae contained the black spots

Table 1. Tergal melanism of female *P. maculiventris* adults treated topically with juvenile hormone as fifth-stage larvae (24 ± 8 h post-ecdysis) and reared under long-day conditions at 26.7°C.

Treatment	N	Melanization Score ($\bar{x}$ ± SEM)
CO_2 control	93	4.39 ± 0.16
5 μg JH-1[a]	13	1.00 ± 0.00
0.5 μg JH-1	29	2.79 ± 0.38[b]
0.05 μg JH-1	73	3.68 ± 0.21[c]

[a] One nymph-adult intermediate obtained and 7 died prior to or during ecdysis.
[b] Fourteen of 15 individuals scored ≥2 had unmelanized patches within areas of melanized cuticle.
[c] Three of 62 individuals scored ≥2 had unmelanized patches within areas of melanized cuticle.

(Aldrich et al., 1981), implicating melanin as the black pigment in this hemipteran. Thus, the black tergal pigment in *P. maculiventris* adults is provisionally referred to as melanin.

The data demonstrate that melanism in *P. maculiventris* adults depends on the temperature experienced by early fifth-stage larvae, with cooler temperatures resulting in more melanic adults. Females are, on the average, more melanized but less melanically variable than are males. Photoperiod has little or no effect on melanization of spined soldier bug adults. In the field, individuals maturing during the warm summer days are less melanized than individuals maturing in the spring and fall. A similar correlation between seasonal temperatures and darkening has been reported for adult *Lygus* bugs (Hemiptera: Miridae), but in these insects the darkening, although irreversible, spreads continuously in the tissue underneath the transparent cuticle with age (Wilborn and Ellington, 1984). Sampling of *P. maculiventris* revealed that adults caught in April were much more melanized than those caught the previous September and October. Since sampling required attraction of adults to a synthetic pheromone, it is probable that late-maturing adults (likely to be melanic) were committed to diapause and unresponsive to pheromone. If this is the case, sampling late in the season is biased toward less melanized individuals.

The reasons for melanic variation in *P. maculiventris* are obscure. In the two-spot ladybird beetle (Brakefield and Willmer, 1985) and other insects (Casey, 1981) geographical and seasonal variation in melanism is involved in regulation of body temperature. Melanin may also serve to shield insects from harmful ultraviolet radiation (Kayser, 1985), and the increased melanization of insects near smoke-polluted cities enhances crypsis (Kettlewell, 1961). Each of these functions seems inapplicable as a rationale for the melanism of spined soldier bugs because the tergum is always covered by the wings when the insects are not flying and the wing cuticle that is exposed renders the bugs cryptic in their forest habitat. Moreover, when laboratory-reared *P. maculiventris* adults held at 15.5°C were set free on a sunny day, they did not open their wings to bask in the sun (unpubl. observation). Although spined soldier bugs are capable of flying at least several hundred meters nonstop (Aldrich et al., 1984 and unpubl. observation), usually the bugs make repeated short flights, a circumstance under which it is doubtful that tergal melanization appreciably affects thermoregulation. Cott (1940) considered the brightly colored terga of certain Hemiptera (e.g. Coreidae, Nepidae) to be adaptive as "flash colors" to startle predators. Even granting that startling

predators confers a selective advantage upon spined soldier bugs possessing an orange tergum (which seems dubious), there must be some counter selection favoring melanism.

Although melanic variation is much greater for *P. maculiventris* males than females, Evans (1982) found that the body size of spined soldier bug females is much more variable than that of males. This suggests that melanic variation in *P. maculiventris* may involve phenomena affected adversely by increasing the ratio of body surface area to mass, such as thermoregulation or desiccation. But, as argued earlier, a thermoregulatory role for melanism in *P. maculiventris* adults seems unlikely. There is some evidence that melanized cuticle in insects is more resistant to desiccation (Kalmus, 1941a, b), a hypothesis now being tested for *P. maculiventris* adults.

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Literature Cited

Aldrich, J. R., M. S. Blum, H. A. Lloyd, and H. M. Fales. 1978. Pentatomid natural products: Chemistry and morphology of the III–IV dorsal abdominal glands of adults. J. Chem. Ecol. 4: 161–172.

Aldrich, J. R., J. A. Svoboda, and M. J. Thompson. 1981. Cuticle synthesis and inhibition of vitellogenesis: Makisterone A is more active than 20-hydroxyecdysone in female milkweed bugs. J. Exp. Zool. 218: 133–137.

Aldrich, J. R., J. P. Kochansky, and C. B. Abrams. 1984. Attractant for a beneficial insect and its parasitoids: Pheromone of the predatory spined soldier bug, *Podisus maculiventris* (Hemiptera: Pentatomidae). Environ. Entomol. 13: 1031–1036.

Aldrich, J. R. 1985. Pheromone of a true bug (Hemiptera-Heteroptera): Attractant for the predator, *Podisus maculiventris,* and kairomonal effects, pp. 95–119. *In* Acree, T. E., and D. M. Soderlund, eds., Semiochemistry: Flavors and pheromones. Walter de Gruyter and Company, Berlin.

Andersen, S. O. 1985. Sclerotization and tanning of the cuticle, pp. 59–74. *In* Kerkut, G. A., and L. I. Gilbert, eds., Comprehensive insect physiology, biochemistry and pharmacology, Vol. 3. Pergamon Press, Oxford.

Blatchley, W. S. 1926. Heteroptera or true bugs of eastern North America. The Nature Publishing Company, Indianapolis. 1116 pp.

Borror, D. J., D. M. DeLong, and C. A. Triplehorn. 1981. An introduction to the study of insects. Saunders College Publishing, Philadelphia. 928 pp.

Brakefield, P. M. 1984. Ecological studies on the polymorphic ladybird, *Adalia bipunctata* in the Netherlands. I. Population biology and geographical variation of melanism. J. Anim. Ecol. 53: 761–774.

Brakefield, P. M. and P. G. Willmer. 1985. The basis of thermal melanism in the ladybird *Adalia bipunctata*: Differences in reflectance and thermal properties between the morphs. Heredity 54: 9–14.

Casey, T. M. 1981. Behavioral mechanisms of thermoregulation, pp. 79–114. *In* B. Heinrich, ed., Insect thermoregulation. John Wiley and Sons, New York.

Cott, H. B. 1940. Adaptive coloration in animals. Methuen and Company, Ltd., London. 508 pp.

Couturier, A. 1938. Contribution a l'etude biologique de *Podisus maculiventris* Say predateur Americain du doryphore. Ann. Epiphyties Phytogen. 4: 95–165.

Curtis, A. T., M. Hori, J. M. Green, W. J. Wolfgang, K. Hiruma, and L. M. Riddiford. 1984. Ecdysteroid regulation of the onset of cuticular melanization in allatectomized and *black* mutant *Manduca sexta* larvae. J. Insect Physiol. 30: 597–606.

Dupuis, C. 1949. On the 'late melanism' of the larval stages of Pentatomidae (Hemiptera Heteroptera). Entomol. Mon. Mag. 85: 229–230.

Evans, E. W. 1982. Timing of reproduction by predatory stinkbugs (Hemiptera: Pentatomidae): Patterns and consequences for a generalist and a specialist. Ecology 63: 147–158.

Hori, M., K. Hiruma, and L. M. Riddiford. 1984. Cuticular melanization in the tobacco hornworm larva. Insect Biochem. 14: 267–274.

Kalmus, H. 1941a. Physiology and ecology of cuticle colour in insects. Nature 148: 428–431.

———. 1941b. The resistance to desiccation of *Drosophila* mutants affecting body colour. Proc. R. Soc. Lond. Ser. B 130: 185–201.

Kayser, H. 1985. Pigments, pp. 367–415. *In* Kerkut, G. A., and L. I. Gilbert, eds., Comprehensive insect physiology, biochemistry and pharmacology, Vol. 10. Pergamon Press, Oxford.

Kettlewell, H. B. D. 1961. The phenomenon of industrial melanism in Lepidoptera. Ann. Rev. Entomol. 6: 245–262.

Knight, H. 1923. Studies on the life history and biology of *Perillus bioculatus* Fabricius, including observations on the nature of the color pattern (Heteroptera, Pentatomidae). 19th Report State Entomologist of Minnesota 1922: 50–96.

———. 1924. On the nature of the color patterns in Heteroptera with data on the effects produced by temperature and humidity. Ann. Entomol. Soc. Am. 17: 158–172.

Novak, V. 1955. Nektere zakonitosti vyvoje ventralnich cernych skvrn u plostice *Oncopeltus fasciatus*. Mem. Soc. Zool. Tchecosl. 19: 233–246.

Truman, J. W., L. M. Riddiford, and L. Safranek. 1973. Hormonal control of cuticle coloration in the tobacco hornworm, *Manduca sexta*: Basis of an ultrasensitive bioassay for juvenile hormone. J. Insect Physiol. 19: 195–203.

Wilborn, R. and J. Ellington. 1984. The effect of temperature and photoperiod on the coloration of the *Lygus hesperus, desertinus* and *lineolaris*. Southwest. Entomol. 9: 187–197.